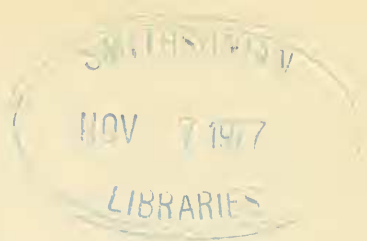


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ELEPHANT SEALS BREEDING ON THE
MAINLAND IN CALIFORNIA

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ABSTRACT: A northern elephant seal gave birth on the mainland at Año Nuevo Point, California, in 1975, the first mainland birth for this species in this century. Seven females gave birth in 1976 and 16 in 1977. The initiation of breeding in this location was apparently precipitated by crowding on the Año Nuevo Island rookery, less than 1 km away. The new breeding area shows signs of increasing rapidly in size. Two hundred and forty-five thousand tourists attempted to view the seals during the last three years; 106,000 were taken on tours. The animals did not appear to be disturbed by the presence of humans in plain view at a distance of 10 m or more.

INTRODUCTION

Northern elephant seals, *Mirounga angustirostris*, breed on offshore islands along the coast of California and Baja California, Mexico. Except when sick or injured, they have rarely been observed on the mainland during this century. However, the population has increased so dramatically during the last decade that space on islands in northern California has come to be in short supply. Male elephant seals began to appear on the mainland directly across a narrow channel from the rookery on Año Nuevo Island, California, during the 1967 breeding season (Poulter and Jennings 1966). They have been seen here in every subsequent breeding season and their number has steadily increased. In 1975, a female came ashore and gave birth on the mainland. To our knowledge, this was the first

northern elephant seal born on the continental mainland during this century. The cyclic, predictable appearance of these huge marine mammals on Año Nuevo Point, a state reserve that is open to the public, has attracted thousands of tourists from nearby metropolitan areas. They have jammed the reserve in recent winters in an attempt to view and photograph the seals. Various confrontations between seals and people, ranging from humorous to dangerous, have occurred.

The purpose of this paper is to trace the history of elephant seals on the mainland in this area, to present data which enables us to speculate on how and why breeding began here, and to discuss the implications of this extension in breeding range for these animals and man.

To fully appreciate the recent appearance of

elephant seals on the mainland, one must consider this development in the context of the species' history over the last 175 years. Thousands of elephant seals existed at the beginning of the 19th century before sealing began. Their breeding range extended from Cabo San Lázaro in Baja California, Mexico, north to Point Reyes, California (Scammon 1874). However, in the space of about 40 years, the elephant seal population was decimated by sealers who killed them for their oil. By 1860, the population was so severely reduced that sealing was no longer economically feasible and, in 1869, the species was considered virtually extinct. The nadir of the elephant seal population was around 1894 to 1900 when less than 20 individuals survived on a single beach on remote Isla de Guadalupe, an oceanic island approximately 300 km off the coast of Mexico (Bartholomew and Hubbs 1960).

In 1922, the species was given protection by the government of Mexico. The United States government gave similar protection a few years later. The number of elephant seals has been increasing logarithmically ever since. They now reoccupy most of their former range. Immigrants from the parent colony on Isla de Guadalupe began to recolonize islands along the coast of Mexico and southern California during the period 1930 to 1950. Colonies in northern California were established on Año Nuevo Island in 1961 (Radford, Orr and Hubbs 1965) and on Southeast Farallon Island in 1972 (Le Boeuf, Ainley and Lewis 1974).

The Año Nuevo Island rookery seems to have reached its carrying capacity. The number of pups born on Año Nuevo Island has increased every year since the first two pups were born in 1961 (Le Boeuf 1977). In 1977, 750 pups were born; at least this many females were present as well as 266 breeding-age males. During the peak of the breeding seasons in 1975, 1976 and 1977, the two sandy beaches on the island were crowded with females, their pups and adult males. Few additional males could have been accommodated on these preferred breeding areas (Le Boeuf and Briggs 1977). Evidently, some animals were affected by the crowded conditions and bred elsewhere. Many of the animals that colonized Southeast Farallon Island, 89 km to the north, during the period 1972 to 1977, were immigrants from Año Nuevo Island (Le Boeuf, Ainley and Lewis 1974; Harriet

Huber, personal communication). Breeding began on the Año Nuevo mainland during this same period.

METHODS

Año Nuevo Island is located 30.6 km north of Santa Cruz, California. It is separated from the mainland point that juts out to sea by a 0.8-km channel. The study area is shown in Figure 1.

Periodic censusing of the Año Nuevo Mainland began during the 1968 breeding season (1 December through 15 March) as an adjunct to systematic studies of the northern elephant seal on Año Nuevo Island by Le Boeuf and collaborators from the University of California at Santa Cruz (e.g., Le Boeuf and Peterson 1969; Le Boeuf and Briggs 1977). This paper covers censuses taken on the mainland during the period 1968 to 1977.

The number of censuses varied greatly from year to year. The mean number of censuses per breeding season from 1968 to 1974 was 22 and the range was from seven in 1973 to 50 in 1971. Counts were made at various times of day, from late December until the first week in March, by walking the beach or from the island using a 15–60 power spotting scope. In 1975 and 1976, censuses were taken one to three times a week, usually in the mornings between 0900 and 1100 hours, by walking the length of the beach and searching the dune area. On several occasions, a second census was taken in the late afternoon. In 1977, censuses were taken daily at 0900 throughout the breeding season.

In our censuses, we distinguished males from females and adults from pups and juveniles. Breeding-age males were separated into four categories: adults (8+ years old), subadult or SA⁴ (7–8 years old), SA³ (6–7 years old), SA² (5 years old) and SA¹ (4 years old). SA¹ males are rarely observed on land during the breeding season (Le Boeuf 1974).

In addition to counting and categorizing the animals, we were able to keep a record of individuals present. Studies on the island necessitated marking all males. This was done by bleaching a name or number into the pelage on both sides of each animal's back as soon as it arrived (Le Boeuf and Peterson 1969) and by attaching numbered plastic tags into the interdigital webbing of the hindflippers (Le Boeuf, Ainley and Lewis 1974). Since most males moved back and forth between the island and the main-

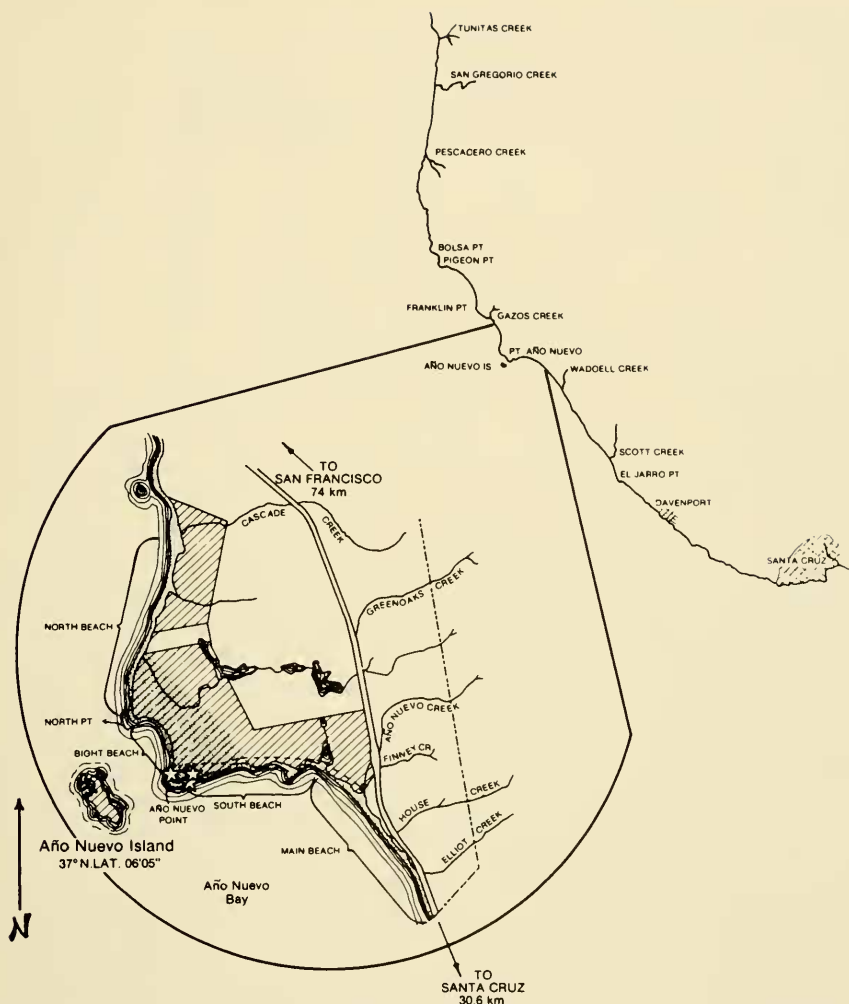


FIGURE 1. A schematic drawing of the Año Nuevo mainland and Año Nuevo Island. Stars indicate the location that females gave birth in 1976. Most of the females that gave birth in 1977 congregated in a harem on the east side of Año Nuevo Point. The state reserve property is lined and the sand dunes are stippled.

land, most seals observed on the mainland were already marked and could be identified individually. When necessary, marking and tagging were also done on the mainland. In 1975, 1976 and 1977, females and their pups were given individual marks (names) and tags denoting their relationship and the time and place of birth. Thus, in addition to determining the number and composition of animals present each day, we could also identify individuals and follow them from day to day and from year to year.

Since 1975, we have paid special attention to reproductive behavior and pup mortality. We recorded the following data on females: the time

of arrival, the date and location of parturition, the sex and condition of pups, the frequency and date of each copulation as well as the male involved, and the date of departure. If an arriving female was tagged, its age could be determined. The location of parturition of all females was determined as well as their nursing behavior. We noted the reactions of females to their own pups and to those of other females. The incidence and manner of pup deaths were recorded.

RESULTS

Number. The number of elephant seals observed on the mainland during the breeding sea-

TABLE 1. NUMBER OF ELEPHANT SEALS ON AÑO NUEVO MAINLAND (ML) AND AÑO NUEVO ISLAND (ANI) DURING A TEN-YEAR PERIOD.

Breeding season	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Highest daily census of males on ML	7	6	3	10	6	18	26	45	64	151
Number of different males on ML per season	7	11	7	15	16	38	44	94	148	320
Number of different males on ANI per season	103	120	125	136	146	180	146	143	227	266
Number of females on ML at peak season	0	0	0	0	0	0	0	1	7	16
Number of females on ANI at peak season	178	219	291	296	341	360	426	556	687	740

son increased dramatically from 1968 to 1977 and coincided with a rapid increase in the size of the colony on the island. Table 1 shows that both the highest daily census and the number of different males observed in a season increased significantly during the study period. No females were observed prior to 1975. The rapid growth of the Año Nuevo Island population is reflected by the annual increase in number of females counted at peak season. The number of pups produced each year was approximately the same as the number of females counted at peak season (Le Boeuf and Briggs 1977).

Distribution. Figure 1 shows the location on the mainland where the majority of seals were observed and the relationship of this area to the island. During the 1967 season, males were observed on Bight Beach and near Año Nuevo Point (Poulter and Jennings 1966). In later seasons the seals occupied an increasingly larger area of the mainland with some individuals appearing beyond the limits of the map shown in Figure 1. However, the majority of animals were observed between North Point and the eastern edge of South Beach; the heaviest concentration was usually in the immediate vicinity of Año Nuevo Point. In recent years movements into the sand dune area became more frequent. On several occasions, males were observed as much as 0.5 km back into the dunes. In 1977, the dunes near Bight Beach were a gathering place for numerous subadult males.

In 1972, males began hauling out on beaches beyond the boundaries of the state reserve. One

early excursion was recorded on national television; a mature bull surfaced on the Pebble Beach Country Club golf course, 72 km from Año Nuevo Island, during the middle of a tournament. He was back on the island the following day. In the same year, one subadult male made numerous trips to Southeast Farallon Island. He and two other males from the Año Nuevo colony became permanent residents of this rookery the following year (Le Boeuf, Ainley and Lewis 1974). In 1974, another bull took up residence for approximately three weeks on the main beach near the park entrance which borders the southern edge of the reserve. In 1975, 1976 and 1977, males were sighted on several other beaches in the vicinity, extending from Bean Hollow Beach, 14.5 km to the north, to Davenport Landing, 14.5 km to the south. Other public beaches where males were observed for several days include: Gazos Creek, Waddell Creek, Scott Creek, and Greyhound Rock (Figure 1). Most of the males observed on these peripheral beaches were mature, i.e., classified as an adult or near adult (SA⁴).

Prior to the arrival of females, spacing between males on the beaches was 3–4 meters or more. Males were rather evenly distributed on Bight Beach, near Año Nuevo Point, and on South Beach. When females began to give birth in the vicinity of Año Nuevo Point (Figure 1), males began to concentrate in this area. This was especially noticeable in 1977 when a harem composed of 12 females formed in this area.

Composition. Who were these males that fre-

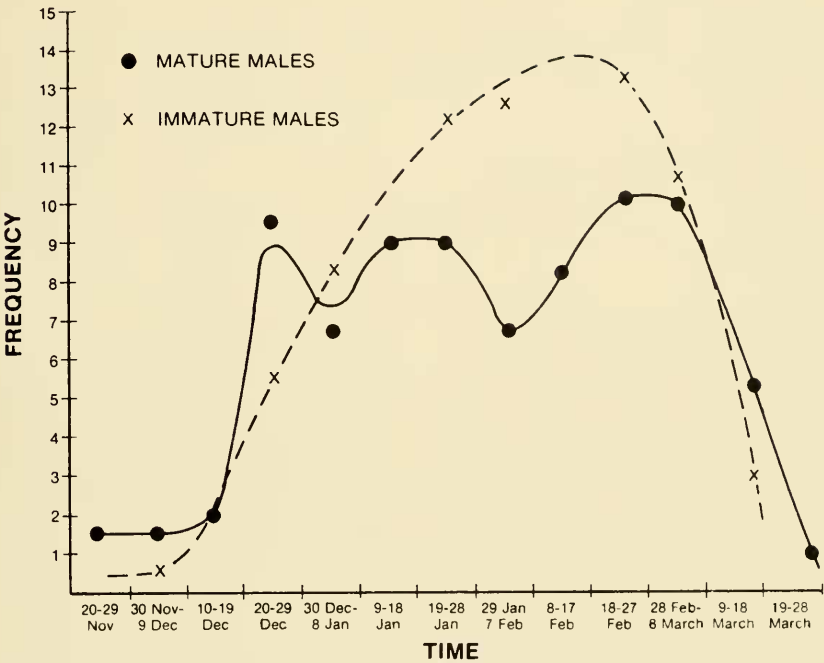


FIGURE 2. The mean number of mature and immature males on the Año Nuevo mainland calculated at 10-day intervals during the 1975 breeding season. A mature male is one who is approximately 8 years old or older.

quented the mainland? Because nearly all of them were marked individually and daily records of their whereabouts were kept, it was evident that males observed on the mainland were associated with the island population. Indeed, many males moved back and forth across the channel on a daily basis. For example, in 1976, 65 percent of the males marked on the island were observed at least once on the mainland; all males observed on the mainland were also seen on the island.

Table 2 shows that both mature and immature males were present on the mainland, with the former predominating in early years. This discrepancy may have been due in part to the fact

that it was more difficult to mark all immature males because they continued to arrive throughout the season. In addition, a greater effort was made to mark adults in early years. On the island, the ratio of mature males to immatures was very close early in the study period. By 1975, immatures were more prevalent than matures on both the island and the mainland. The ratio of adults to immatures on the island in 1974 is inconsistent with other years because of a reduced effort to mark young males. In general, the age composition of males observed on the mainland reflected the age range of males that were present on the island.

Mature males tended to outnumber immature

TABLE 2. NUMBER OF MARKED MATURE (ADULTS AND SA⁴ MALES, 7 YEARS OF AGE OR OLDER) AND IMMATURE BULLS (SA² AND SA³ MALES, LESS THAN 7 YEARS OLD) HAULED OUT ON AÑO NUEVO MAINLAND AND ISLAND IN TEN CONSECUTIVE BREEDING SEASONS.

Area	Age Category	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Mainland	Mature	4	9	5	8	10	23	31	46	55	58
	Immature	2	2	2	7	6	15	11	48	93	262
Island	Mature	41	46	50	51	50	74	89	69	75	71
	Immature	48	56	64	60	77	92	49	74	152	195

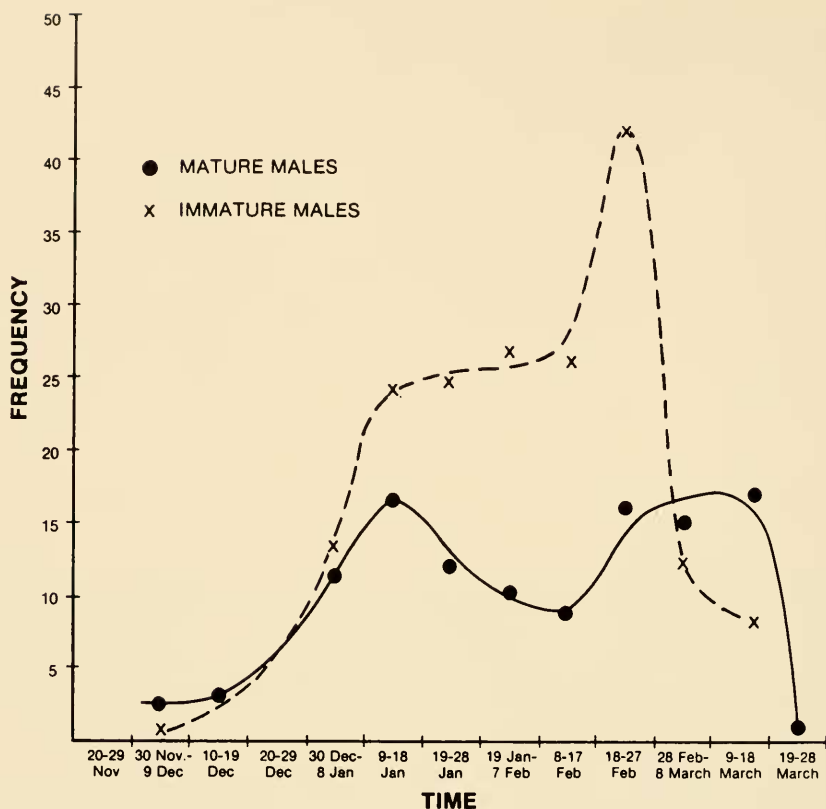


FIGURE 3. The mean number of mature and immature males on the Año Nuevo mainland during 10-day intervals in the 1976 breeding season.

males during the beginning and end of each breeding season. The distribution of males on the mainland in 1975 and 1976 is shown in Figures 2 and 3. This difference in distribution with age was due to multiple causes. One strategy of adult males was to rest on the mainland in December and early January and then move to the island in late January when females began coming into estrus. Some individuals were very predictable and repeated this pattern from one year to the next. Movement from the mainland to the island by the older, more dominant males was particularly evident in late January and early February. This pattern was less in evidence in 1977.

The peak number of immature males on the mainland occurred in mid-February and coincided with the time of highest copulatory activity on the island (Figures 2 and 3). This pattern resulted in part from the fact that many young males were chased off the breeding beaches on the island by older, more aggressive bulls when

the majority of females came into estrus. Thus, the young males were forced to haul out on various non-breeding areas on the island and on the mainland. This pattern of immature males reaching a peak on the mainland in mid-February was most obvious from 1974 to 1976. Figures 2 and 3 also show that immature males arrived on the mainland later in the season, and they left earlier than adult males.

Once females began to appear on the mainland, the most dominant males tended to remain near the females until the latter had given birth, nursed their pups, copulated and returned to sea. Only then did the males cross the channel to compete for females on the island. At season's end, when all females had departed from the island, some males returned to the mainland to rest before going out to sea.

Another strategy that was observed, particularly in early years, was for adult males to rest on the mainland for several days or even a few weeks after losing an important fight on the is-

TABLE 3. REPRODUCTIVE SUCCESS OF MAINLAND-OBSERVED MALES ON AÑO NUEVO ISLAND.

Breeding season	1968	1969	1970	1971	1972	1973	1974	1975	1976
Number of different males on ML per season	7	11	7	15	16	38	44	94	148
Number of different ML-observed males that copulated on ANI	2	4	4	4	6	12	14	39	34
Percent copulations by ML-observed males on ANI	5	4	20	no data	19	31	6	68	42

land. Several former harem masters on the island, deposed after commanding a harem containing hundreds of females for as long as six weeks, recuperated in exile on the mainland. The sight of bloody bulls prompted local residents and tourists to refer to the mainland as "loser's beach." This is misleading. Clearly, some males were resting after having been defeated in a fight, but many of them on the mainland were by no means losers from the point of view of aggression or reproductive success. Table 3 shows that at least a quarter of the males observed on the mainland each year copulated on the island. In 1975 and 1976, males that had been seen on the mainland accounted for 42 and 68 percent of the copulations observed on the island. Furthermore, in every year of the study, at least one male observed on the mainland was among the 10 highest ranking bulls on the island. The correlation between rank and reproductive success among males is high and positive (Le Boeuf 1974). Finally, we can reiterate that the majority of the males in the Año Nuevo population were observed both on the island and on the mainland.

As the total number of males on the mainland increased over the course of the study period, males began to arrive earlier and stay later in the season each year. In 1968, the first male arrived on 11 January and the last one left on the first of March. In 1977, the first male arrived on 15 November and the last one departed on 26 March.

Non-reproductive behavior of males. There were no obvious differences in the behavior of mature and immature males on the mainland. Most of them spent their time sleeping on the dry sand near the upper edge of the beach. A few rested among the sand dunes. Threatening behavior, chasing and an occasional fight were frequent activities of waking animals even before

females began to appear. After the females arrived, aggressive encounters were most frequent in their vicinity. Young males were not as aggressive as older males and one might say that they "played" like adults in these aggressive confrontations. On several occasions, males attempting to land were rebuffed by the threats of dominant males on land—the result was that they landed further up or down the beach. This pattern of competition for social rank is typical of males on the island (Le Boeuf 1971, 1974). Many movements on the mainland consisted of simply going in and out of the water. Most often, this was in response to aggressive encounters with other males, but the animals also entered the water to cool off in hot weather. Males were often observed swimming along the surf line checking out the opposition, chasing off subordinates with the characteristic vocal threat, and remaining silent and low in the water when swimming past a dominant male.

Duration of stay. The duration of each male's stay on the mainland was variable. Some males were sighted on the mainland only briefly. Others crossed the channel several times a day and were sighted at several disparate locations. Some individuals remained in virtually the same location for several weeks. For example, in 1974, an aging bull named Star caused us considerable trouble because he spent most of the breeding season sleeping on a narrow sandy access road to the beach, the route that we had to drive over in order to launch our boat to the island. The presence of females on the mainland after 1975 did not appear to change significantly the duration of the mainland haul-out for the majority of males; the exceptions were the few males who did most of the breeding.

Reproductive activities on the mainland. On 21 January 1975, a pregnant female hauled out near Año Nuevo Point (Figure 1). Three days

later she gave birth to a female pup. A pregnant female had attempted to land here in 1973 but she was frightened off by tourists. The birthplace and age of the new mother were unknown. She and her pup were tagged and named, Bertha and Blue, respectively. Bertha nursed her pup daily for 30 days. A mature male, Baja, remained near here throughout the nursing period and kept all other suitors away. He alone, apparently, copulated with her on the same day that she returned to sea. All of these activities were similar to those seen on the island (Le Boeuf, Whiting and Gantt 1972), except that they were performed under the watchful eyes of thousands of tourists (e.g., San Francisco Chronicle, 29 January 1975; San Jose Mercury, 18 March 1975).

The 1976 breeding season. Bertha and six other females gave birth on the mainland in January, 1976. Three additional females were observed and marked in the area early in the month but they remained for only a day or two before departing.

The age and birthplace of only one mainland female was known. She was a three-year-old, born on Año Nuevo Island and tagged (Green tag 1961) as a one-month-old weaned pup on 13 February 1973. Her pup died when it was 11 days old after being trampled by a charging bull. This female left the area later in the day.

Besides the above, another female gave birth to a full-term stillborn. Thus, two pups died out of the seven born on the mainland. The other five pups survived to weaning and remained on the mainland for a few weeks after all adults had departed.

An additional pup, a 1½-week-old orphan found at Drake's Bay near Point Reyes, was transported to the Año Nuevo mainland on 26 January by representatives of the California Marine Mammal Center, Fort Cronkhite, California. They placed the orphan alongside Bertha who was pregnant. She adopted the alien pup, allowing it to suckle along with her own pup who was born later in the evening. Both the adopted orphan and the filial pup survived to weaning age. The topic of adoption will be treated in more detail in a later section.

In 1976, mainland females gave birth in three separate locations (Figure 1): three gave birth on the beach just north of Año Nuevo Point, two on South Beach and two in the sand dunes, approximately 20 m inland from South Beach. Once

females landed and gave birth they tended to remain in the same place throughout the 3–4 week nursing period without ever entering the water. This is characteristic of all nursing elephant seals (Le Boeuf, Whiting and Gantt 1972). The female whose pup was born dead was an exception. She was observed going in and out of the water several times as well as moving from one mainland harem to another.

The most dominant male on the mainland was named Up and he spent most of the season near the females on Año Nuevo Point. He alone copulated with both females that came into estrus. The next two males in order of dominance were SRI-236 and Atom. They positioned themselves near the females on the South Beach and near those in the dunes, alternating positions from time to time, particularly early in the season. Atom copulated with one female and SRI-236 copulated with two other females in the area. The three top-ranking males on the mainland were all adults. SRI-236 was ten years old, having been born and tagged on Año Nuevo Island in 1966 (Poulter and Jennings 1966). He was next seen on the island during a breeding season in 1971. Up and Atom were approximately the same age, and they were first observed on Año Nuevo Island in 1972. All three males returned to the island in subsequent breeding seasons and all of them were first observed on the mainland in 1974. The social behavior of other males on the mainland was concentrated around the breeding females and tended to be similar to that displayed by males competing on the island.

The 1977 breeding season. The number and distribution of males and females on the mainland underwent an obvious change in 1977. The population more than doubled, and for the first time a harem formed on the mainland at Año Nuevo Point consisting of 12 females at peak season. The number of males observed in the area was more than double that of the previous year, the increase being primarily in the subadult male category. The older, larger males concentrated on Año Nuevo Point near the female harem. Subadult males were more widely scattered except for a group of 50 to 60 individuals that congregated regularly in the sand dune area near the center of Bight Beach.

Sixteen females gave birth on the mainland in 1977, the original female, Bertha, being one of them. All births occurred during the interval 12 January to 6 February. As in the previous year,

TABLE 4. INTERVALS IN DAYS BETWEEN FEMALE REPRODUCTIVE EVENTS ON THE ISLAND AND THE MAINLAND.

	Año Nuevo Island			Año Nuevo Mainland	
	1970 ¹	1971 ¹	1976 ²	1976 ³	1977 ⁴
Arrival to parturition	—	6.5 ± 1.4 (10)	6.3 ± 1.6 (29)	3.3 ± 0.8 (6)	4.0 ± 1.6 (14)
Parturition to 1st copulation	24.6 ± 3.4 (9)	23.4 ± 4.2 (12)	26.1 ± 1.8 (25)	23.8 ± 3.3 (4)	22.8 ± 2.2 (13)
Parturition to departure (nursing period)	27.9 ± 4.0 (12)	29.0 ± 5.0 (29)	27.3 ± 1.6 (48)	26.0 ± 2.7 (5)	25.9 ± 1.1 (14)
1st copulation to departure	3.3 ± 2.8 (9)	5.2 ± 2.2 (11)	3.1 ± 1.9 (27)	4.0 ± 3.5 (4)	3.6 ± 2.3 (13)
Arrival to departure	34.3 ± 3.6 (10)	34.6 ± 3.8 (9)	32.4 ± 2.8 (17)	27.8 ± 3.8 (4)	29.9 ± 1.7 (14)

¹ From Le Boeuf, Whiting and Gantt (1972).

² Unpublished data collected by B. Le Boeuf, K. Panken, M. Pierson and J. Reiter.

³ Excludes Green tag 3503 who gave birth and lost her pup. She did not nurse until 19 days later when she adopted a weaner. She departed 38 days after parturition and was on the mainland a total of 41 days.

⁴ Excludes two females who abandoned their pups, one on the day it was born and the other seven days later. They both went to sea on the day they abandoned their pups.

several additional females landed early in January but did not remain in the area long nor did they give birth.

Besides Bertha, only one female from the previous year returned to the mainland to give birth (Green tag 3503). Two females that gave birth on the mainland in 1976 gave birth on the island in 1977 (Green tags 1861 and 3501). One female that gave birth on the mainland in 1977 (Green tag 1880) had given birth on the island in 1976. Of the three females that switched locations, two were three-year-olds who had lost their pups in the earlier year.

Tags on four females revealed that they had been born on Año Nuevo Island in 1973 and 1974. Thus, three females were primiparous three-year-olds, and one of them was a four-year-old.

Four females did not join the harem on Año Nuevo Point (Figure 1). Bertha and an unmarked female gave birth in the dunes approximately 100 meters east of the harem at Año Nuevo Point. However, Bertha entered the harem site before leaving the rookery. A three-year-old female and another female (Green tag 4543) gave birth on South Beach approximately 50 meters east of the harem.

There were no pup deaths on the mainland in 1977.

A male named BTLF (Green tag 3405) dominated all other males on the mainland, and he was involved in 60 percent of the matings ob-

served. He was the first male to mate with 12 of the 16 females present. Most of the copulations by other males were performed while BTLF was engaged in combat with a challenger. BTLF was retagged on Año Nuevo Island during the 1975 breeding season; his earlier tag broke and could not be read. He copulated 29 times on the island in 1976 and was responsible for 4.7 percent of the matings observed. Up, the alpha male on the mainland in 1976, returned to the mainland in 1977 but copulated only once.

Female vital statistics. A comparison of intervals between various reproductive events on the mainland and the island reveals several differences (Table 4). For nearly every comparison the interval is shorter for mainland females than for females giving birth on the island. Compared to island females, mainland females gave birth sooner after arriving, they copulated sooner after parturition, they nursed their pups at least one day less, and they spent less total time on land during the breeding season. All comparisons between the 1976 island data and the 1977 mainland data are statistically significant (*t*-tests, *p* < .05) except for the interval, first copulation to departure.

Sex ratio of pups. Of the 24 pups born on the mainland during 1975 to 1977, 10 were males and 14 were females. The sample size is too small to permit a meaningful test for a significant deviation from the 50:50 sex ratio. The sex ratio of pups born on the island has not deviated signifi-

TABLE 5. THE FREQUENCY OF VARIOUS TYPES OF NURSING RELATIONSHIPS OF FEMALES ON THE MAINLAND.

	1976 (N = 7)	1977 (N = 16)	Both years combined (N = 23)
<i>Nursed own pup to weaning age</i>			
a. exclusively	2	6	8
b. and an alien occasionally	0	3	3
c. and an alien as well	2	5	7
<i>Nursed an alien after losing own pup</i>			
a. exclusively (adoption)	1	0	1
b. occasionally			
<i>Did not nurse (because pup died, was abandoned, lost or stolen)</i>	2	2	4

cantly from unity in recent years (Le Boeuf and Briggs 1977). It is notable that all four three-year-old females gave birth to female pups; a four-year-old female gave birth to a male.

Maternal behavior. The most frequently observed nursing relationship in elephant seals is one in which the mother nurses her own pup to weaning and rejects the suckling attempts of alien pups. However, several deviations from this pattern occur (Le Boeuf, Whiting and Gantt 1972). Indeed, complications in the nutritive relationship between females and pups on an elephant seal rookery were quite evident in the small and, hence, easily observed aggregation of females breeding on the mainland. Although it is beyond the scope of this paper to analyze this complex phenomenon in detail, we will describe some of these relationships to give the reader an appreciation for the range of possibilities observed.

In 1976, an aggressive female with pup stole the newborn of a neighbor and nursed it, plus her own pup, to weaning age. The neighbor remained in the harem without nursing for 19 days and then adopted a weaned pup on the day its mother left the harem. She nursed the large weaned pup, a male, for 20 days. In contrast, two other females departed the area on the day their pups died. Bertha, as we have already mentioned, adopted an orphan before she gave birth to her own pup; she nursed both pups to weaning age. Only two of seven females nursed their own pups exclusively.

Additional complications were observed in 1977. Although the majority of females nursed only their own pups, five females nursed an alien pup in addition to their own. One of them involved the serial adoption of two pups. While nursing her own pup, this female adopted an orphan and nursed it for three days where upon she adopted another orphan, which she nursed for 12 days. Bertha, again, fostered a pup in addition to her own. Two females that gave birth within one day of each other nursed each other's pup as well as their own. Finally, two females abandoned their pups one and seven days after parturition, respectively. Their pups were nursed to weaning age by two different females with pups of their own. In both years, it was obvious to us that pups sharing a mother weighed less at weaning age than pups that suckled a female by themselves. However, weights were not obtained which would confirm this impression.

The variety of nursing relationships observed on the mainland and the frequency of their occurrence are summarized in Table 5. It is interesting to compare these figures with those collected on Año Nuevo Island in 1970 and 1971 by Le Boeuf, Whiting and Gantt (1972). In this study, 72 percent of the females in a sample of 50 nursed their own pups to weaning age (alone or in addition to an alien pup). This figure is similar to the figure obtained on the mainland in 1976 and 1977, i.e., 78.3 percent of the 23 females nursed their own pups to weaning age. However, the percentage of adoptions was more than twice as high on the mainland as on the island, 34.8 percent of the females adopted a pup on the mainland compared to 14.0 percent on the island. We conclude that adoption occurs if a female nurses a pup consistently for one or more days regardless of whether she is already nursing her own pup. The duration of fostering observed on the mainland ranged from 7 to 26 days. Ten percent of the females in the island study did not nurse any pup after giving birth as compared to 17.4 percent in the mainland sample. None of these females were ever observed copulating. Finally, in the larger population on the island, a few females each year permitted several pups to attempt to nurse at the same time. This permissiveness was not observed in mainland females, perhaps because there were fewer orphans present at all times.

Non-breeding season observations. Prior to

1976, the only observations of elephant seals on the mainland during the non-breeding season was in March and April. An occasional weaned pup swam across the channel and rested on the mainland for a few days, or a molting juvenile appeared for an equally short stay. However, in June 1976, many young males, who normally molt on the island at this time of year, were observed resting on the mainland at Bight Beach (Figure 1). For example, on 11 June, 20 males were resting on the mainland and 25 were in the water offshore. The highest number counted on-shore was 30 on 26 June (M. Bradeen, personal communication). Elephant seals are observed on Año Nuevo Island at all times of the year (Le Boeuf, Ainley and Lewis 1974). Perhaps the presence of subadult males in June 1976 signals the beginning of a similar pattern on the mainland.

The reaction of seals to humans. Prior to the 1974 breeding season, the presence of elephant seals on the mainland attracted little attention. Only a few local residents and nature lovers knew about the seals and paid much attention to them. The distance of the seals' resting place from the parking lot was also a deterrent. Año Nuevo Point is about a 30-minute walk from the park entrance, and it can be cold, wet and windy in winter. However, just before the start of the 1974 breeding season, a national magazine called attention to this unusual spectacle and recommended it to its readers (Sunset Magazine, December 1973). Suddenly, this rather desolate area was flooded with hundreds of tourists. The understaffed and underfinanced Department of Parks and Recreation was not prepared to deal with this huge influx of people. During that winter, people were free to roam the beaches and dunes, and only the number entering the reserve was controlled. On one fair-weather weekend, as many as a thousand people strolled the beaches and sand dunes in the vicinity of Año Nuevo Point. Each male elephant seal was surrounded by a circle of onlookers and amateur photographers. Families with small children walked too close to bulls weighing as much as 2–3 tons, unaware of the danger. Some people giggered, prodded and threw pebbles at these giants in order to get more interesting photographs. The public had not been informed that these animals might be dangerous or sensitive to human disturbance. In retrospect, it is surprising that no one was injured. We know of several

cases where people have been bitten by elephant seals at other places (the second author is one of them).

It is equally surprising that the seals, all males that year, were so impervious to this constant attention and frequent harassment. Their typical response was to sleep and occasionally flip sand on their backs. When irritated, they gave a low-level open-mouth threat and increased the frequency of their sand flipping habit (Heath and Schusterman 1975). When pushed even further, some bulls reared up and bellowed the species-typical threat vocalization. Some charged the attacker for a distance of a few meters. Despite being provoked most males remained on the beach. Even those young males who backed down and were hounded into the water returned to the beach a short time later. Regardless of the throng of people in the area, the seals appeared to be primarily interested in each other's movements. Several times it looked as if a male was charging a human when in reality he was attacking another male behind the person. When the seals were not being disturbed or approached too closely, they seemed to ignore the humans in the area.

Disturbance to the seals in the park reserve was reduced considerably in subsequent years. Beginning in 1975, tourists were led on guided tours of the seals in groups of 20. Park rangers and student guides were informed about the animals, and were prepared to answer questions about them. A single path led through the sand dunes to overlooks near Año Nuevo Point and South Beach where the incipient harems were located. Tourists were restricted to the paths and overlooks and were prohibited on the beaches and dunes where the animals were abundant. Approximately 245,000 people came to view the seals during the winter months of 1975, 1976 and 1977; approximately 106,000 people were led on tours.

It is difficult to say whether a constant stream of tourists in plain view of the seals inhibited utilization of this area by the seals. Males did not appear to be affected very much even when harassed (a response that made them easy to slaughter in the last century). Females, on the other hand, are much more wary, especially when they first arrive and before they give birth. If disturbed during this period, females may reenter the water and either return to the same location later or give birth elsewhere. This pat-

tern has been observed on the island in previous years (Le Boeuf, Whiting and Gantt 1972). We do not know whether females were frightened off by human activities on the mainland and, if so, the numbers that were affected. Since females often survey a potential breeding beach from the water before hauling out, this form of disturbance is difficult to monitor. Some females haul out and then leave. We know of at least three pregnant females that landed on the mainland in 1976 and subsequently departed before giving birth. A similar pattern was observed in 1977. We do not know what caused these females to leave, and we were not able to determine where they gave birth.

Once a female gives birth, her movements decrease significantly and she is not likely to abandon her pup even if disturbed or approached closely by a human. Under these circumstances, a female will flip sand on her back nervously, issue a vocal threat and then attack. She will bite, hold and shake the victim. Female bites can produce severe injury. We saw several instances on the mainland where tourists ventured close enough to females and their pups to provoke arousal of females and the threat reaction just described. When advised, park rangers increased the viewing distance between seals and humans and this form of disturbance and potential danger was eliminated. When humans and seals were separated by approximately 10 m or more, the seals appeared to acclimate to the presence of humans in plain view, and females did not show obvious signs of alarm. As far as we could tell, the response of females to their pups was not affected adversely by human presence, but this subject deserves systematic study.

DISCUSSION

The initiation of breeding on the Año Nuevo Mainland is a reflection of the continued growth and recovery of the northern elephant seal population following its near extinction in the last century. Indeed, the growth of the population has increased so rapidly of late that the Año Nuevo Island breeding beaches have become filled to capacity at peak season (Le Boeuf and Briggs 1977). It is this condition which seems to have precipitated breeding in what might be called a suboptimal area—suboptimal because the mainland was formerly a habitat in which the seals were subjected to predation from carnivores and coastal aborigines. Several lines of

evidence lead to this conclusion: 1) females did not begin breeding on the mainland until the breeding beaches on the island began to be crowded (Le Boeuf and Briggs 1977); 2) during the same period, a new colony was formed on nearby Southeast Farallon Island, with most of the original settlers coming from Año Nuevo Island; and 3) on Año Nuevo Island, the first females to arrive at the start of the breeding season have been observed preventing later arriving females from landing (Christenson and Le Boeuf 1977) or forcing them to occupy peripheral positions in harems where pup mortality is higher (Le Boeuf and Briggs 1977).

Preliminary data suggest that it is the youngest females that begin breeding in new areas. Many of them are literally prevented from landing on breeding beaches or they are relegated to inferior locations by older, more aggressive females. Older females do this to enhance the probability of their own pups surviving (see Le Boeuf and Briggs 1977). A female is fully grown at six years of age; however, developing females usually give birth for the first time at age three, a few as early as age two. Subsequently, females give birth to a single pup annually (Le Boeuf, unpublished data). Most of the marked females breeding on Southeast Farallon Island from 1972 to 1977 were between three and six years old. For example, four of six known-age females that gave birth in 1975 were four years old, the other two were three years old and five years old, respectively. As late as 1977, seven females out of 12 known-age newcomers were three or four years old (H. Huber, personal communication). On the Año Nuevo mainland, four of the known-age females that gave birth were three years old and one was four. Furthermore, observations of known-age females on Año Nuevo Island in 1976 by us, J. Reiter and M. Pierson revealed that over 50 percent of the females five years of age or less became separated from their pups, while less than 10 percent of the females six years of age or more lost their pups. Since mother-pup separation is the initial event in a syndrome culminating in pup mortality (Le Boeuf, Whiting and Gantt 1972; Le Boeuf and Briggs 1977), reproductive success, as measured by pup survival, is evidently lower in young females than in older females who are fully grown. Thus, it is obviously a reasonable strategy for young females to explore breeding in a peripheral place with more space, less competi-

tion from older, more aggressive females and, in effect, a place where there is a higher probability that their pups will survive.

Several discrepancies in behavior observed between females breeding on the island and those breeding on the mainland appear to be a consequence of the younger age of the latter. The shorter nursing period and reduced time spent on land during the breeding season by mainland females (Table 4) is consistent with the smaller size of young females. Small females are more severely limited by their body reserves while nursing (and at the same time, fasting completely) than larger females. Furthermore, the high percentage of adoptions we observed among mainland females seems to reflect their youth and inexperience. This relationship is supported by observations of young females on the island.

That only males were present indicates a wholly non-breeding use of the mainland prior to 1975. The pattern of utilization by males was much like that which we observed in non-breeding areas on Año Nuevo Island and in other rookeries; that is, it was a place for males to rest and a base from which they could make periodic forays into harems to enter into mating competition with other males. We consider the mainland as simply a new breeding area for the already established Año Nuevo colony and stress that the mainland aggregation should not be considered a new colony. The establishment of a new colony develops in quite a different way. On Southeast Farallon Island, juveniles hauled out during the spring and fall for several years before adults began to appear in winter and breeding began. Females were the first to appear during the initial breeding season, just the opposite of the situation that obtained on the Año Nuevo mainland (Le Boeuf, Ainley and Lewis 1974).

A characteristic trait of most elephant seal females is to return to the same location to give birth year after year (Le Boeuf, Whiting and Gantt 1972). Because of this habit, the abundance of sandy beaches on the mainland, and the fact that the Año Nuevo Island colony continues to increase in size despite the virtually complete utilization of breeding space on the island, we expect that the number of females breeding on the mainland will increase rapidly in the near future. During the last ten years, the mean annual increase in pups born on the island

was 16.9 percent with a range of 3 to 31 percent (Le Boeuf and Briggs 1977). Future increments in pup production within the colony will probably be borne by the mainland, especially since the Southeast Farallon Island colony, which has received immigrants from Año Nuevo Island for the past six years (Le Boeuf, Ainley and Lewis 1974; H. Huber, personal communication), is fast approaching its carrying capacity. In short, we expect that the size of the breeding unit on the mainland will increase very rapidly. If conditions are not altered drastically, we project that over 1,000 pups will be born there within the next decade.

The possibility of such a great increase in the number of seals breeding at this location will provide the public with a resource that is recreational, informative and unique. The abundance of tourists that have come to view these animals here in the past few years attests to public interest. Numerous busloads of children from elementary and high schools for miles around have taken field trips to this area. There is no other place in the United States where breeding pinnipeds can be viewed so easily and from such close quarters. State and federal officials will have to anticipate continued growth of this seal colony and prepare both for the protection of these animals and for full and imaginative utilization of this natural phenomenon as a resource of great interest and education for the public.

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